

# The Genomic Drive Hypothesis and Punctuated Evolutionary Taxonations, or Radiations

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## Abstract

Orthodox evolutionary theory does not accord with what palaeontologists usually find in the fossil record, which mainly indicates long periods of stasis, interspersed with relatively short periods of rapid change, that is, macro or micro punctuational evolutionary taxonations. This is usually known as punctuated equilibrium. A novel hypothesis we have called Genomic Drive, points towards Transposable Elements (TEs) as powerful facilitators of evolution and as essential for induction of periodic changes in the rate of evolution. The Genomic Drive hypothesis, which is supported by current data, if confirmed, will open the way for the reconciliation of evolutionary theory with the findings of most palaeontologists. It may also help to explain the extraordinary fecundity of some orders, and the paucity of species in others, and why there are “fossil species”.

**Keywords:** Evolution; the Genomic Drive hypothesis; transposable elements; taxonations; punctuated equilibrium; gradualism; stasis; extinction; fossil record

## Introduction

Discovered by Barbara McClintock in the 1950s (McClintock 1950, 1956, 1984), TEs were authoritatively written off thirty years later as parasitic, junk, or selfish DNA, which we would be better off without (Orgel & Crick 1980; Doolittle & Sapienza 1980). However, during the last decade a large number of researchers have noted that the evolutionary potential of taxa can benefit from the presence of TEs (Kidwell & Lisch 2001; Bowen and Jordon 2002; Kazazian 2004; Feschotte & Pritham 2007; Goodier & Kazazian Jr. 2008) and many others. Building on this foundation, we developed the Genomic Drive hypothesis, the major elements of which were recently published as an unnamed synthesis (Oliver & Greene 2009).

Genomic Drive, according to our hypothesis, is a powerful facilitator of evolution in sexually reproducing eukaryotes. It is the process by which germ line or early embryo genomes engineer coding, regulatory, karyotypic, or other changes to their own genome. Transposable elements (TEs) (see Table 1) are the major facilitators of evolution by Genomic Drive (Oliver & Greene 2009). Other genomic content, such as simple sequence repeats (SSRs) also make some contribution (Kashi & King 2006; King *et al.* 2006). Of course we do not deny that many other factors also facilitate evolution and may possibly result in punctuation events on some occasions. Some examples are: whole genome duplications, endosymbiosis, horizontal gene transfer (especially in bacteria) point mutations, insertions and

deletions, and other such well known phenomena. We also acknowledge that their may be some as yet unknown phenomena that help to facilitate evolution and that may also give rise to punctuation events. We present Genomic Drive as a hypothesised major facilitator of evolution, but certainly do not claim that there are no other significant facilitators of evolution. Indeed, some phenomena such as point mutation highly complement Genomic Drive by allowing newly engineered DNA sequences to diversify. A notable example of this is the ape-specific *GLUD2* gene, which encodes a glutamate dehydrogenase enzyme involved in neurotransmitter recycling. Derived from a retrotransposed copy of *GLUD1* that has undergone critical nucleotide substitution events, *GLUD2* appears to have significantly increased the cognitive powers of the apes (Burki & Kaessmann 2004).

## Major Principles of the Genomic Drive Hypothesis

TEs (Transposable Elements) are ubiquitous, comprising 20% to 80% of most genomes, and are extremely ancient; they are powerful facilitators of evolution. We have proposed this powerful facilitation of evolution by TEs, as the Genomic Drive hypothesis. Successful taxa do not destroy TEs, but strongly control transposition of TEs in the soma, where they are often damaging and cannot be inherited. However, they allow some TE activity in the germ line and the early embryo, where they can generate potentially useful variation in progeny, for natural selection to work on. Thus Genomic Drive can cause genetic changes of great magnitude and variety within germ line genomes, making such genomes flexible and dynamic, so that they drive their own



Table 1

## A Brief Summary of the two Types of Transposable Elements (TEs)

Type I Transposable Elements are retrotransposons or retroposons (retro-TEs) which transpose via an RNA intermediate, in a “copy and paste manner” by means of an encoded reverse transcriptase protein (RT), and other protein(s) encoded in the autonomous LINES (Long Interspersed Nuclear Element), LTRs (Long Terminal Repeats), and ERVs (Endogenous Retroviruses). The non-autonomous SINEs (Short Interspersed Nuclear Element) which have internal promoters use the reverse transcriptase of the LINES to transpose and multiply. Retrocopies (Processed pseudogenes or PPs) can also be transposed by reverse transcriptase, helping to facilitate evolution, but cannot multiply further, as they lack promoters.

Type II DNA Transposons (DNA-TEs) of most superfamilies transpose by a “cut and paste” mechanism. They encode various transposases, according to their family, which recognises their terminal inverted repeats (TIRs) and transposes them from one location in the genome to another, sometimes with an increase in copy number.

evolution and the evolution of their resultant phenotype. Genomic Drive can cause many genomic alterations that cannot be caused by any other mutagens. The de novo synthesis of new, or orphan, genes from TEs, and perhaps other non-coding DNA, has recently been confirmed in fruit fly and humans. Genomic Drive can build, sculpt, and reformat genomes by both active and passive means. Active Genomic Drive is due to the active transposition of TEs, from either a heterogeneous or homogenous population of TEs. Passive Genomic Drive is due to ectopic recombinations between homologous TE insertions. Such ectopic recombinations are common only when there are large homogeneous populations of TEs. TEs can infiltrate germ lines by endogenous de novo synthesis, e.g. SINEs, SVAs, by exogenous invasions by retroviruses e.g. ERVs and LTRs, and by horizontal transfer between taxa, mostly by DNA-TEs. New infiltrations of germ line genomes by TEs, or modifications to existing TEs, or various stresses experienced by the phenotype, can result in intermittent bursts of TE activity. We propose that this can result in punctuational evolutionary taxonations or radiations, usually known as punctuated equilibrium.

Although sometimes harmful to some individuals, TEs can be very beneficial to lineages. The result of this is lineage selection for lineages endowed with a suitable repertoire of TEs; this endows such lineages with enhanced evolutionary potential. Taxa or lineages deficient in active TEs, and with heterogeneous populations of inactive TEs, tend to be non-fecund, tend to prolonged stasis, and eventually may become extinct. Conversely, taxa or lineages well endowed with such TEs tend to be fecund, or species rich, as they taxonate readily. This could be called the evolution of evolvability. Cellular defences against excessive TE activity have resulted in the capacity of genomes to evolve epigenetic controls of TEs, which may further facilitate evolution or adaptation by epigenetic means.

In short, TEs, which we propose constitute the main engine of Genomic Drive, can result in the generation of widely divergent new taxa, fecund lineages, lineage selection, and punctuated equilibrium (Oliver & Greene 2009). Others, to give but one example, Goodier & Kazazian (2008), have clearly recognised the likelihood that bursts of TE transposition could accelerate taxonation, and that evolution has been adept at changing “junk” into treasure. However, they have stopped short of developing any hypotheses to this effect, and exploring the implications of such hypotheses.

## Gradualism and Punctuated Equilibrium

Gradualism and Punctuated Equilibrium are two possible modes of evolution. Current orthodox evolutionary thought is dominated by an assumption that biological lineages evolve by the slow and gradual accumulation of adaptive mutations, that is, by gradualism, and that macroevolution (the origin of higher taxa) can be explained by an extrapolation of microevolution (the origin of races, varieties and species) into the distant past (Kutschera & Niklas 2004; and many others). This line of thought has been mostly dominant since Charles Darwin who, influenced by Lyell’s concept of very slow changes in geology, regarded gradualism as fundamental to his theory. Darwin unreservedly said *Natura non facit saltum* (nature does not make a leap). Despite a number of early dissenters such as Bateson in the 1890s who strongly advocated evolution by discontinuous variation or sudden leaps, gradualism was eventually incorporated into neoDarwinism and the Modern Synthesis (Bowler 2003). However, many palaeontologists have found that gradualism does not concur with the majority of the fossil record. Instead, new species are found to arise abruptly and periodically and there are intermittent and often long periods of stasis, punctuated by periods of rapid change and branching speciation. These punctuations often occur during different periods in diverse lineages, so are apparently not always related to environmental changes. The observed persistence of ancestors in stasis, following the abrupt appearance of a descendant, is an indicator of punctuated equilibrium (Eldridge & Gould 1972; Stanley 1981; Eldridge 1986, 1995; Gould 2002). This is not to be confused with the hypothesis that fairly rapid, but gradualistic, evolution can occur in peripheral isolates, followed by the movement of the resulting new taxon back into the main population, giving the erroneous appearance of a gap in the fossil record.

Punctuated equilibrium, as detailed by the palaeontologists cited above, has been observed in certain very fine grained strata, and entails intermittent periods of rapid evolutionary change, over an estimated 15,000 to 40,000 years (Gould 2002), which gives birth to a new taxon that remains little changed (i.e. in a period of stasis) until it becomes extinct, usually four to ten million years later. This taxon is often the progenitor of other taxa in the same lineage, while it is still extant. Contemporaneous, or successor taxa, in the same lineage eventually suffer the same fate. Of course, mass extinction events can interrupt this pattern, but they only



account for less than 5% of all extinct species and recovery from them tends to be slow, about 5 million years in the Early Triassic, after the end of Permian great mass extinction (Erwin 2001). This seems to make the “Cambrian explosion” seem all the more remarkable. That gradualism occurs sometimes is not denied, and Fortey (1985), from a study of Ordovician trilobites, estimated that the ratio of punctuated equilibrium type speciation to gradualist speciation is 10:1, while Ridley (2004) posits that although both occur, and punctuated equilibrium appears to be the more common, they may be extremes of a continuum. It seems, therefore, that the ratio of these types of speciation events, one to the other, is somewhat uncertain. According to Gould (2002), punctuated equilibrium should not be confused with the hypothesised evolution of “hopeful monsters” by saltations (Goldschmidt 1940). Whereas many palaeontologists have observed punctuated equilibrium, they could not explain it satisfactorily in terms of the Modern Synthesis. Now, however, intermittent waves of transposable element activity have very recently been hypothesised to be a major causal factor of punctuated equilibrium (Oliver & Greene 2009; Zeh *et al.* 2009; Parris 2009), seemingly finally reconciling evolutionary theory to punctuated equilibrium, and the fossil record. However, whereas Zeh *et al.* (2009) place heavy emphasis on environmental stress as a trigger for TE activity, we additionally consider *de novo* emergence (e.g. SINEs) activating modifications, especially to promoter regions (e.g. LINEs and SINEs), horizontal transfer of TEs, and germ line invasions by retroviruses, as intermittent events that can trigger new waves of TE activity (Oliver & Greene 2009). Parris (2009) suggests intermittent germ line invasions by retroviruses, possibly in concert with environmental change, as an example of a trigger for intermittent rapid taxonation. There are many examples of such intermittent waves of TE activity temporarily accelerating evolution, such as the amplification peaks of the now extinct L2 LINEs and MIR SINEs roughly coinciding with the marsupial-eutherian split ~120–150 Mya, and the peak activity of the L1 LINEs corresponding to the early eutherian radiation ~100 Mya (Kim *et al.* 2004). *Myotis* (a genus of microbats) is one of the most species rich mammalian genera and Stadlemaun *et al.* (2007) found that a burst of *Myotis* diversification occurred ~12–13 Mya corresponding well to the estimated time during which the most active DNA-TE families were expanding in the *Myotis* genome (Ray *et al.* 2008).

#### Transposable Elements have Periodic Waves of Activity

Although retro-TEs can horizontally transfer between taxa only very rarely, new infiltrations of germ lines by retro-TEs can occur by *de novo* synthesis of SINEs, the fusion of SINEs into dimers, or the fusion of SINEs with other complex elements. Activating modifications to SINEs, and to the untranslated (promoter) regions of LINEs can also occur, and so on. Invasions of the germ line by exogenous retroviruses are also common, as are modifications to existing endogenous retroviruses or retroviral remnants. All of these intermittent events can result in transient waves of retrotransposition. Such intermittent waves of transposition often result in contemporaneous waves of retrocopies or retrogenes

(these are sometimes called processed pseudogenes) which can sometimes be converted into useful new genes by other mutations. SINEs (especially Alu SINEs) are also thought to be typically activated in response to stresses on the host organism (Oliver & Greene 2009; Zeh *et al.* 2009). These waves of retrotransposition can therefore activate periods of rapid evolution punctuating the more normal near stasis of a taxon, giving punctuated equilibrium type evolution. In contrast to retro-TEs, many DNA-TEs can readily transfer horizontally from one taxon to another, sometimes between widely divergent lineages. There is often a dramatic wave of TE activity following on from a horizontal transfer event (Pace *et al.* 2008). However, all transposable elements, both Type I and Type II, can eventually succumb to the increased effectiveness of cellular controls such as methylation and interfering RNAs, and to crippling mutations which can eventually result in much reduced activity, and a possible return to near stasis in the affected taxon. But there are nearly always periodic new infiltrations of TEs in genomes by one means or another, to keep Genomic Drive going and to intermittently result in rapid evolution. If this does not occur then, according to the Genomic Drive hypothesis, extinction of the affected taxon is likely, if all other things are equal, or alternatively the taxon could become a fossil species. This is in agreement with the fossil record where extinction, aside from the mass extinctions, is the normal eventual fate of a taxon, but usually the lineage to which it belongs, survives. An example of this is the hominid lineage, where a number of earlier successful hominids which were in stasis, showing little variation over time, such as *Homo erectus*, succumbed to extinction but where *Homo sapiens* both survives and thrives (Eldridge 1986).

#### Genomic Drive in Mammals

The Human Genome is composed of about 45% TEs: ~42% are retro-TEs, made up of ~21% LINEs, ~13% SINEs, ~8% LTRs and ERVs. Most, but by no means all, of these are inactive, so some active Genomic Drive is continuing in humans. However, as nearly all of the LINEs are L1s and nearly all of the SINEs are the primate-specific Alu SINEs, there is a good potential for passive Genomic Drive, by means of such repetitious DNA promoting ectopic recombinations. A wide variety of DNA-TEs make up the other ~3% of TEs in the human genome, all of which are inactivated molecular fossils, but some have been exapted for cellular functions and are under positive selection, as in the *SETMAR* chimeric primate (anthropoids only – not prosimians) gene (Cordaux *et al.* 2006). TEs do cause disease in individuals, but in humans only slightly more than 0.5% of known genetic diseases are attributable to TEs. With ~356 extant species the primates are moderately fecund. Bursts of considerably increased TE activity have been associated with the major separations and divergences in the primate lineage, such as those of prosimians and Old World monkeys, and of Old World monkeys and apes (Oshima *et al.* 2003; Kim *et al.* 2004; Khan *et al.* 2006).

Quite atypically for mammals, the bats have many recently active DNA-TEs, some of which may be still active, as well as retro-TEs (Ray *et al.* 2007, 2008; Pritham & Feschotte 2007). Bats are correspondingly fecund, and with approximately 1000 extant species they comprise over 20% of all mammalian species. Bats evolved in an



early Eocene “big bang” ~52 million years ago (Simmons 2005) and appear to have taxonated rapidly. Rodents exhibit even greater fecundity, comprising close to 40% of all extant mammals, and these are well endowed with retro-TEs, but in at least some rodents (mice) individuals apparently pay a high price for the success of their lineage, as they have very many more TE-caused genetic diseases in individuals than do humans (Maksakova 2006). The bat and rodent orders contrast with the colugos, or “flying lemurs” (order Dermoptera) with only 2 to 4 species, but little is known about their TEs at present, except that they lack the 7SL derived SINEs that may have been a major factor in the successful radiations of the rodents and primates. More data on the genomes of colugos would be very valuable in assessing the consistency of their paucity of species with the Genomic Drive hypothesis.

With punctuated equilibrium evolution, as evidenced in the fossil record, stasis is the normal condition, and rapid change occurs rarely. Stasis is data, which must be accounted for in a satisfactory theory of evolution. “Living fossils” such as the Tuatara and the Coelacanth have been more or less in stasis for hundreds of millions of years. Information about the TEs in their genomes is scarce, but what there is suggests that these species have a paucity of TE activity, which is entirely consistent with the Genomic Drive hypothesis (Oliver & Greene 2009). The robustness of the Genomic Drive hypothesis as applied to the evolution of other phyla has scarcely even been contemplated, but there is certainly evidence of long periods of stasis in some insects, and in crocodilians.

### The Genomic Drive Hypothesis and Plants

TEs are also very active in plants and some angiosperm genomes are comprised of up to ~80% TEs. We have not yet extensively investigated the validity of the Genomic Drive hypothesis for plant evolution, but preliminary investigations indicate that plants also show punctuated equilibrium type taxonation. Plants have their fecund lineages, such as orchids in the monocots and daisies in the dicots, among the very numerous angiosperms, which evolved ~130 million years ago. Plants also have “fossil species” like the gymnosperm *Ginkgo biloba*, which has leaves similar in form and venation to those found in rocks deposited in the Mesozoic era (248–65 Mya) when ginkgo-like plants apparently had a worldwide distribution (Foster & Gifford 1974). Gymnosperms, which evolved ~350 million years ago, have relatively few species and seem to be in stasis, but are still very successful in terms of biomass, forming extensive forests in both the northern and southern hemispheres. Hybridisation giving sterile plants, followed by polyploidy to give fertile plants, is an observable and well documented example of punctuated equilibrium. The endosperm has also played a significant role in the evolution of many angiosperms by means of possible reproductive isolation caused by mismatches of the endosperm balance number (Johnson et al. 1980). The Genomic Drive hypothesis, when its probable application to plants is thoroughly investigated, may also help to explain the major transition of the angiosperms from their possible seed fern progenitors. However, another factor to consider is that the large advances in plant evolutionary forms are all associated with high global

CO<sub>2</sub> levels at different periods of the earth’s history (Calver et al. 2009).

## Conclusions

Genomic Drive is a new hypothesis which still needs much development and testing, but it powerfully portrays the profound effects that waves of transposable element activity produce in intermittently driving evolution, and also the possible passive effects of homogenous repertoires of inactive TEs. Much evidence suggests that it offers an explanation for stasis, and for rapid punctuational evolutionary taxonations and/or radiations, or punctuated equilibrium as it is usually called, as has been found in the fossil record. However, like all hypotheses it needs to be subjected to testing. If it is confirmed, it will offer a new conceptual foundation for much of evolutionary theory and will probably enable a reconciliation of the findings of palaeontologists with biological evolutionary theory which has not been possible previously. It also seems likely that it, when fully developed, will be able to help to explain why some lineages are very fecund, while other lineages are quite non-fecund and why some lineages evolve rapidly while others linger in stasis and terminate in “living fossils,” and similar puzzles. Working out the relationship between TEs and evolution, in terms of cause and effect, seems likely to be a fruitful area of research well into the foreseeable future.

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